

Temporal fluctuations in scale counts and body proportions of Amazonian riparian lizards (*Cnemidophorus*, Sauria, Teiidae)

by

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Abstract

Abrupt but short-lived changes in number of ventral rows of scales and of dorsal granules, as well as in relative length of tail, tibia and head, were found in widely separated riverine populations of Amazonian *Cnemidophorus*, both parthenogenetic and bisexual. The explanation adopted is that offered by CARSON (1985) for a similar case in Hawaiian *Drosophila*: presence of considerable intra-clonal variability and sensitivity to stabilizing selection.

Keywords: Lizards, riverine, parthenogenetic, variability, selection, Teiidae, Sauria, Amazon, Neotropics.

Resumo

Mudanças abruptas, mas de curta duração, foram encontradas no número de fileiras de escamas ventrais e de grânulos dorsais, bem como no comprimento relativo da cauda, da tibia e da cabeça, em populações ribeirinhas, bissexuais e partenogenéticas, de lagartos do gênero *Cnemidophorus* na Amazonia brasileira. A explicação adotada é aquela oferecida por CARSON (1985) para um caso similar de *Drosophila* no Hawaii: presença de considerável variabilidade genética intra-clonal e sensibilidade a seleção estabilizadora.

*Dedicated to Prof. Dr. Harald Sioli on the occasion of his 90th anniversary.

Introduction

In the years 1965 to 1977, this Museum operated the "Expedição Permanente da Amazônia" (EPA), which consisted of a barge for living and working, the "Garbe", towed by a small river boat, the "Lindolpho R. Guimarães". Scientific crews rotated, and the expedition would stop on the riverside and collect, including purchase of specimens from local people. Large series were secured of many species.

Lizards of the genus *Cnemidophorus* are extremely common in and around towns in Amazonia; we obtained good collections both of bisexual and of parthenogenetic populations of what is currently called the *Cnemidophorus lemniscatus* "complex" (FROST & WRIGHT, 1988). The taxonomy of Amazonian *Cnemidophorus* is not yet well understood (e.g., AVILA-PIRES, 1995: 499; COLE & DESSAUER, 1993), and I have been appraising the materials at hand for a tentative review of geographical variation. I routinely checked for homogeneity among samples from localities represented by more than one collection (with a view to combining them), and unexpectedly discovered temporal fluctuations of some meristic characters and body proportions. This report summarizes these patterns.

Materials

The Map shows localities from which *C. lemniscatus* samples were collected, and Table 1 summarizes collecting dates and sample sizes.

Oriximiná (01°46'S, 55°51'W). A sizable town (about 5,000 inhabitants at the time of collecting), on the left bank, some 30 km above the mouth of the Rio Trombetas, a tributary of the Amazonas on its left (north) bank. This is the place where the first parthenogenetic Amazonian population of *Cnemidophorus* was discovered (VANZOLINI 1970). The parthenogenetic populations have not been formally named, but are known by their cytotypes; the Oriximiná cytotype is designated B (PECCININI-SEALE 1989). COLE & DESSAUER (1993) identify this population as belonging to their *C. cryptus*. We collected there nine times between 1965 and 1973, and Prof. Miguel T. Rodrigues, University of São Paulo, made a further collection in 1993.

Alter do Chão (02°32'S, 54°57'W). A small town on the right bank of the Rio Tapajós (a tributary of the Amazonas from the south), some 10 km above the mouth. We made two collections there. The population is bisexual, referable to *C. lemniscatus* (L., 1758) (COLE & DESSAUER 1993).

Breves (01°41'S, 50°28'W). Another sizable town, about the size of Oriximiná, on the landward (western) end of the large island of Marajó (that plugs the mouth of the Amazonas), on the strait named after the town. The population is parthenogenetic; its cytotype is B, as in Oriximiná (PECCININI-SEALE 1989) and the lizard should thus be *C. cryptus*. Breves was visited twice.

Corcovado (01°39'S, 50°32'W). A very small settlement some 8 km to the northwest of Breves, on the same bank as the strait. The lizard population is of parthenogenetic cytotype B, and thus *C. cryptus*. In spite of the close geographical proximity to Breves and of the coincidence of cytotypes, samples collected at both localities on the same day (September 9, 1969) differed significantly in the number of femoral pores, fourth toe lamellae, and dorsal granules. Corcovado was visited twice, on the same occasions as Breves.

In all 674 specimens were used, and from practically all localities we have large samples (Table 1). In some cases subsamples of 20 or 50 specimens were chosen at random for taxonomic work, depending on the variability of the most variable character. Of course it has always been possible to increase the subsamples, but no dubious results made that necessary: all statistical tests gave clear responses.

Characters

I examined four meristic characters in the analysis: (i) the number of transverse rows of ventral scales, counted between the interbrachial series and the anal flap; (ii) the total number of femoral pores; (iii) the number of infradigital lamellae on toe IV, of either side; (iv) the number of dorsal granules, counted transversely at midbody. These are characters routinely used in teiid taxonomy, and known to be reliable. In fact, as can be seen in the tables below, coefficients of variation are unvaryingly low.

Three body proportions were studied: tail length (regression on body, or snout-to-vent, length), length of tibia (regression on body length) and length of head (regression on trunk, or snout-to-vent minus head, length).

Methods

This is essentially a statistical investigation. It is my belief that zoological systematics demands conceptually simple methods, close to the physical nature of the characters. The present issue consists of comparing meristic and morphometric characters of two or more samples from the same locality, taken at different times. In the case of two samples I have used *t*-tests for the differences between means or regression statistics. In the case of three or more samples I used analysis of variance, followed, when adequate, by Tukey's test. The methods used are available in elementary texts, such as DIXON & MASSEY (1983), ZAR (1999) or VANZOLINI (1993).

The following conventions have been adopted throughout:

- a: regression constant (intercept) $\pm$ its standard deviation
- b: regression coefficient (slope) $\pm$ its standard deviation
- df: degrees of freedom
- F: variance ratio
- m: mean $\pm$ its standard deviation
- n: individuals in sample
- R, R (x), R (y): ranges
- r²: coefficient of determination
- s: sample standard deviation
- t: Student's, the quotient of a statistic by its standard deviation
- V: coefficient of variation
- ns: not significant at the 5% level
- *: significant at the 5% level
- ** : significant at the 1% level
- ***: significant at the 0.1% level

In the case of Tukey's test, vertical lines on the left of the table encompass samples that do not differ significantly.

Analysis

We have time series from four localities (Table 1): Oriximiná (10 collections), Alter do Chão and Corcovado (3 apiece) and Breves (2).

Oriximiná

The samples are well suited to statistical analysis. They comprise (Table 6) specimens of all sizes (= ages),

from hatchlings, 29-33 mm in body length, to large adults, over 70 mm. The statistics of the scale counts are shown on Table 2, those of the regressions on Table 6.

The coefficients of variation (V) of the scale counts are uniformly low (1.0 to 4.6) even in the samples with very few individuals. Analysis of variance of the scale counts (Tables 3 and 4) indicates temporal heterogeneities in two characters, number of ventral scales and of dorsal granules. In Tukey's test the statistics are sorted in ascending order. In this analysis (Table 5) I arranged the samples in temporal order and treated them as in Tukey's test: samples that do not differ significantly are encompassed by continuous lines on the left of the table. It is clear that in the case of granules the heterogeneities did not involve any abrupt breaks, but that, in the case of ventrals, 1968b and 1972 are exceptional samples, especially the former. In the 136 days between January 13 and May 28 there was a shift in the mean of the ventrals, with a return to "normal" values within a further 92 days (Fig. 1).

It is interesting to note that the sample means of ventrals and granules are correlated ($F = 22.301^{**}$, $r^2 = 0.7360$, 18 df). No other pair of variables is so correlated, neither are any pair of variables within samples.

The regressions of length of tail and length of tibia (Table 6) are, as usual in lizards, excellent, with the exception of sample 1967b, composed of 5 very young individuals, which did not afford a significant regression. The regressions of head length on trunk length are somewhat less good: the 1967b sample fails again to provide a significant regression.

The study of regressions is divided in two phases, the first is tests the homogeneity of the slopes; if heterogeneities are found the analysis stops. Otherwise the intercepts are tested and, in this case, simultaneous comparison of significant regressions (Table 7) indicates significant heterogeneity in the cases of head x trunk (slope) and tail x body (intercept). Tukey's tests (Tables 5, 8; Figs. 2, 3) reveal in both cases breaks inside the year 1967 and between 1967 and 1968.

Breves and Corcovado

These two localities are geographically very close (ca. 8 km), and are topographically and ecologically identical. On two occasions they were visited on the same (September 19, 1969) or practically the same day (30 July - 2 August, 2-4 August 1968). This opens an interesting possibility of study, as discussed below.

Table 9 summarizes the statistics of the distributions of frequencies of the scale counts for both localities. The two columns on the right of the table refer, respectively, $t(B)$ to the differences between the 1968 and 1969 Breves samples and $t(B \times C)$ to the differences between Breves and Corcovado collected during the same visit. It is seen that in three characters, pores, lamellae and granules, the two localities differed both in 1968 and 1969. Samples from Breves showed significant differences between the two visits in ventrals and granules. Table 10 shows that only the distribution of granules in Corcovado varied in the interval studied, and that 1968 was the outlying year.

Table 12 presents the statistics of the regression analyses. Table 13 shows that in Breves the two years differ in the three regressions: in tail and head length the difference is in intercept, in length of tibia it is in slope. The analysis of variance for Corcovado is shown on Table 14, and Table 11 summarizes the situation in this locality; there are significant heterogeneities in the number of granules, and 1968 is the distinctive year. In the case of Breves it is possible only to say that the differences appeared between 1968 and 1969. In Corcovado, however, in the case of the body proportions, there were heterogeneities both in the regression of tail on body and of tibia on body; in both cases the break occurred between 1968 and 1969.

Alter do Chão

Tables 15 and 17 show the statistics of the distributions of scale counts and of regressions of the only bisexual locality. In both tables the columns headed t refer to sexual differences for the character in the individual years. Tables 16 and 18 contain the respective analyses of variance and Table 19 the application of Tukey's test. It is clear that in the seven comparisons made (granules for females and the three regressions, for both sexes) there was a break within the year 1968. In fact, within this year the break caused even a change in the sexual dimorphisms, in the number of ventrals and in the regression of head

length on trunk length.

Summary

Table 20 summarizes the changes in the characters studied, specifying the time of change, although this was not ascertainable in the case of dorsal granules in Oriximiná.

The salient facts seem to be:

1. Changes occurred in polygenically determined characters.
2. They occurred both in parthenogenetic and bisexual populations.
3. The geographical compass is ample: there are some 600 kilometers between Oriximiná and Breves. In fact, the whole geographical space sampled was involved.
4. Several of the changes were practically synchronous in distant localities.

Comments

It must be avowed that the present findings, however interesting, are fortuitous. The collections were made on general principles and analyzed much later. The analysis was made looking for changes in time, but in truth without much hope of finding any (not quite as a matter of mere form, but frankly of seamliness). Furthermore, in a field where cytological and biochemical information are paramount, we are limited to a few scale counts and body measurements. Thus much cannot be made of the case, but some points deserve comment, as contributing to the rich and difficult field of speciation in Amazonian *Cnemidophorus*.

An analogous case has been reported by CARSON (1985), in which abrupt changes were noticed, with subsequent return to norm. He followed a population of the Hawaiian *Drosophila silvestris* from 1976 to 1980; his paper presents measurements of the foreleg tibia and counts of the cilia on three rows on the same tibia. It is possible from Carson's Table 2 and Figure 1, to recover the data necessary for an analysis of the type adopted here. I have done so and found out that, while tibial length and number of cilia on row 6 remained constant in the time interval sampled, cilia on rows 5 and 5a showed parallel increases in 1979 and a return to previous values in 1980. It was Carson's conclusion that these findings indicated the presence of considerable genetic variability in some quantitative traits and their sensitivity to stabilizing selection. I think the same explanation applies to the present case.

Cnemidophorus is a speciose genus (ca. 50 species) with a high incidence of parthenogenetic lineages. This has stimulated a considerable amount of research on its genetics and evolution (e.g., see papers in WRIGHT & VITT 1993; DAWLEY & BOGART 1989). One of the issues that has been considered in the literature is the contrast between intra-clonal and inter-clonal variability. DESSAUER & COLE (1989), for instance, state that "there is very little individual variation within lineages of unisexual species as compared with bisexual species". This is clearly not the case with Amazonian *Cnemidophorus*: the parthenogenetic and bisexual populations behave in the same way, and both reveal a considerable stock of genetic variability in some quantitative traits, which is reflected in phenotypic plasticity. This is also indicated by the significant differences found between the neighboring localities of Breves and Corcovado in the same day. I think these facts will have to be taken into account in studies of speciation

in the group.

A final issue is the simultaneous occurrence in 1968 of phenotypic shifts in localities as far apart as Oriximiná and the west coast of Marajó. There are two *prima facie* explanations for this synchronism. Either there was a powerful pan-Amazonian ecological phenomenon operating at the time, or this type of occurrence is rather common, and the coincidence just that, a coincidence.

I was on site when all changes occurred, and did not notice any ecological peculiarity. Additionally, having in mind that the explanation might be linked to abrupt massive immigration, I checked the records of the level of the Rio Negro at Manaus, and found no signs of unusual floods. I think, as does CARSON (1985) that such sudden phenotypic shifts are, as said, due to high genetic variability and sensitivity to selection, and that they are not more often noticed because nobody looks for them.

A final issue, and not a trivial one is one practical import of this find: what constitutes a proper geographical sample? Should the concept of time (the moment of collection) be introduced into alpha systematics? Different occasions may mean different phenotypes - the differences possibly reaching a magnitude judged significant in studies of geographical differentiation. This is an unavoidable issue. The presence of stabilizing selection, i.e., the impermanence of the morphological changes, suggests that it would take much bad luck to hit upon a significantly contaminating shift in characters across a geographically meaningful area, but the admonition stands.

Acknowledgments

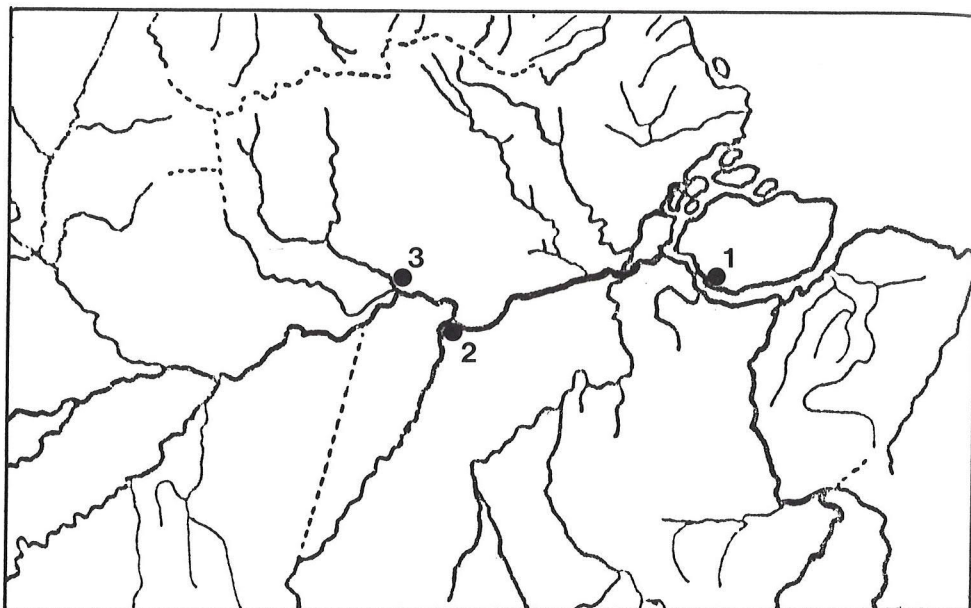
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It is an honor and a pleasure to participate in this homage to Harald Sioli, whose pioneer work on Brazilian limnology is outstanding both for its scientific quality and for its importance to the country.

References

- AVILA-PIRES, T.C.S. (1995): Lizards of Brazilian Amazonia (Reptilia: Squamata). - Zool. Verhandl. Leiden **299**: 1-706.
- CARSON, H.L. (1985): Genetic variation in a courtship-related male character in *Drosophila silvestris* from a single Hawaiian locality. - Evolution **39**(3): 678-686.
- COLE, C.J. & H.C. DESSAUER (1993): Unisexual and bisexual whiptail lizards of the *Cnemidophorus lemniscatus* complex (Squamata: Teiidae) of the Guiana region, south America, with the description of new species. - Amer. Mus. Novit. **3081**: 1-30.
- DAWLEY, R.M. & J.P. BOGART (1989): Evolution and ecology of unisexual vertebrates. - Bull. New York State Mus. **466**: 302 pp.
- DESSAUER, H.C. & C.J. COLE (1989): Diversity between and within nominal forms of unisexual teiid lizards. - In: R.M. DAWLEY & J.P. BOGART (eds.): Evolution and ecology of unisexual vertebrates: 49-71.
- DIXON, W.J. & F.J. MASSEY, jr. (1983): Introduction to statistical analysis. - Fourth ed. McGraw-Hill, Inc., New York: 678 pp.
- FROST, D.R. & J.W. WRIGHT (1988): The taxonomy of uniparental species, with special reference to parthenogenetic *Cnemidophorus* (Squamata: Teiidae). - Syst. Zool. **37**: 200-208.

- MORITZ, C., BROWN, W.M., DENSMORE, L.D., WRIGHT, J.W., VYAS, D., DONNELLAN, S., ADAMS, M. & P. BAVERSTOCK (1989): Genetic diversity and the dynamics of hybrid parthenogenesis in *Cnemidophorus* (Teiidae) and *Heteronotia* (Gekkonidae). - In: R.M. DAWLEY & J.P. BOGART (eds.): Evolution and ecology of unisexual vertebrates: 87-112.
- PECCININI-SEALE, D.M. (1989): Genetic studies on bisexual and unisexual populations of Amazonian *Cnemidophorus*. - In: R.M. DAWLEY & J.P. BOGART (eds.): Evolution and ecology of unisexual vertebrates: 241-251.
- PRICE, A.W., LAPOINTE, J.L. & J.W. ATMAR (1993): The ecology and evolutionary implications of competition and parthenogenesis in *Cnemidophorus*. - In: J.W. WRIGHT & L.J. VITT (eds.): Biology of whiptail lizards (genus *Cnemidophorus*): 371-410.
- VANZOLINI, P.E. (1970): Unisexual *Cnemidophorus lemniscatus* in the Amazonas valley: a preliminary note (Sauria, Teiidae). - Papéis Avulsos Zool., S. Paulo, **23**(7): 63-68.
- VANZOLINI, P.E. (1993): Métodos estatísticos elementares em sistemática zoológica. Hicitec, S. Paulo: 130 pp.
- VRIJENHOEK, R.C. (1989): Genetical and ecological constraints on the origin and establishment of unisexual vertebrates. - In: R.M. DAWLEY & J.P. BOGART (eds.): Evolution and ecology of unisexual vertebrates: 24-31.
- WRIGHT, J.W. (1993): Evolution of the lizards of the genus *Cnemidophorus*. - In: J.W. WRIGHT & L.J. VITT (eds.): Biology of whiptail lizards (genus *Cnemidophorus*): 27-77.
- WRIGHT, J.W. & C.H. LOWE (1968): Weeds, polyploids, parthenogenesis and ecological distribution of all-female species of *Cnemidophorus*. - Copeia **1968**(1): 128-138.
- WRIGHT, J.W. & L.J. VITT (1993): Biology of whiptail lizards (genus *Cnemidophorus*). - Oklahoma Mus. Nat. Hist. Norman, Oklahoma: 417 pp.
- ZAR, J.H. (1999): Biostatistical analysis. - Prentice-Hall, Upper Saddle River: 663 pp.



Map:
Localities: 1: Breves and Corcovado; 2: Alter do Achão; 3: Oriximiná.

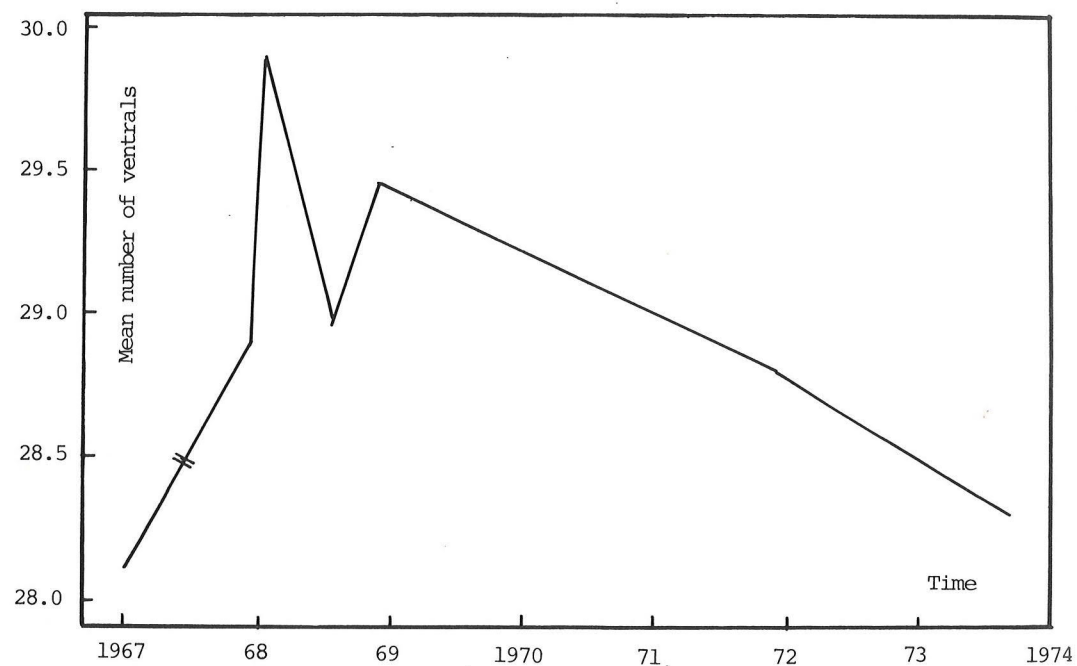


Fig. 1:
Cnemidophorus, Oriximiná, changes in the number of rows of ventral scales with time.

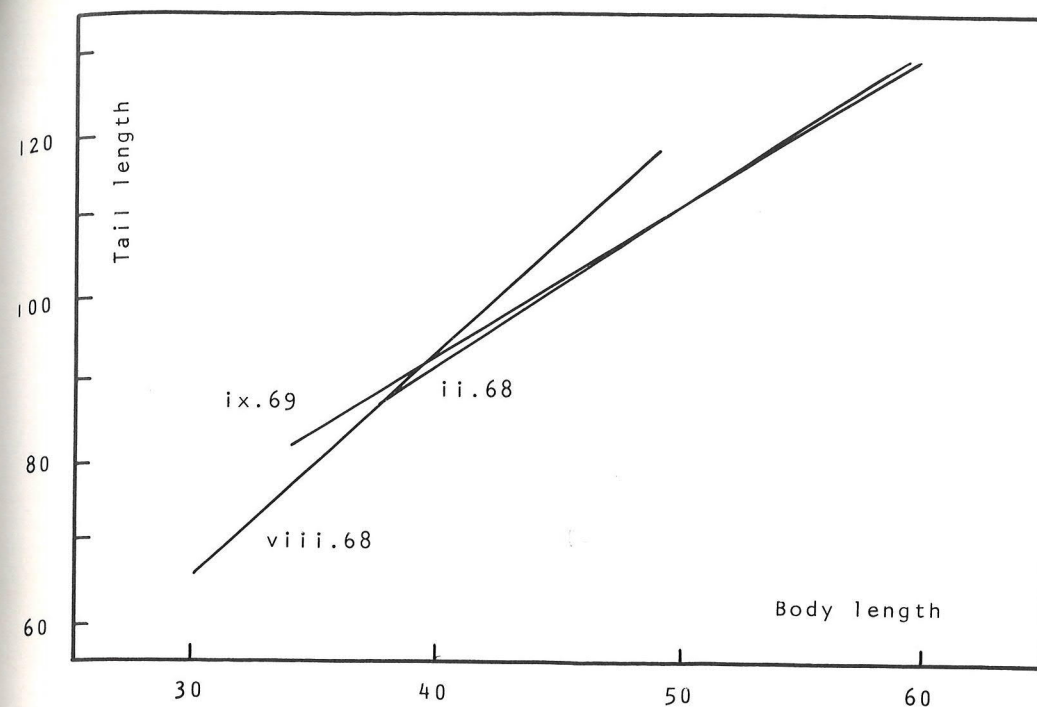


Fig. 2:
Cnemidophorus, Oriximiná, regression of tail length on body length.

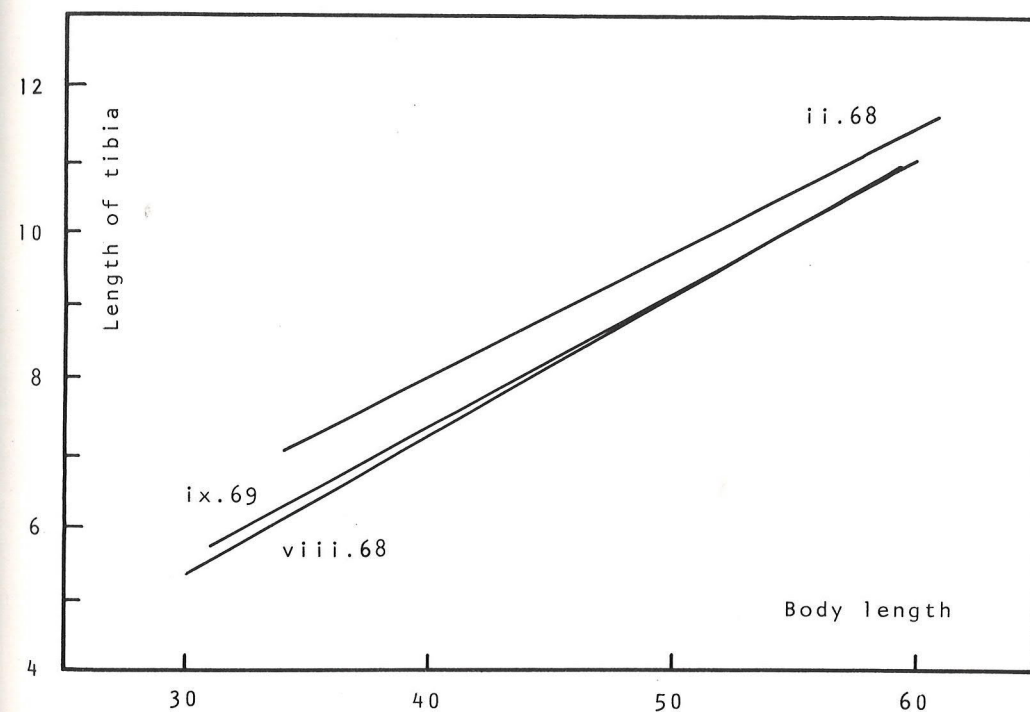


Fig. 3:
Cnemidophorus, Oriximiná, regression of length of tibia on body length.

Table 1: *Cnemidophorus*, materials.

Locality	Date	Code	♂♂	♀♀
Oriximiná	19 September 1965	1965		5
	8 - 24 January 1967	1967a		70
	11 February 1967	1967b		5
	12 - 13 January 1968	1968a		47
	28 May 1968	1968b		10
	28 August 1968	1968c		67
	18 November 1968	1968d		39
	4 - 8 January 1972	1972		20
	3 - 7 November 1973	1973		20
	21 - 31 January 1993	1993		20
Breves	2 - 4 August 1968	1968		50
	9 September 1969	1969		50
Corcovado	18 - 19 October 1965	1965		79
	30 July - 3 August 1968	1968		50
	9 September 1969	1969		50
Alter do Chão	21 - 22 February 1968	1968a	30	30
	17 - 21 July 1968	1968b	30	30
	19 September 1969	1969	30	30

Table 2: *Cnemidophorus*, Oriximiná, Statistics of the distributions of frequencies of the scale counts.

Sample	N	R	m	s	V
Ventrals					
1965	5	28 - 30	28.40 ± 0.400	0.89	3.2
1967a	70	28 - 31	29.04 0.080	0.67	2.3
1967b	5	29 - 30	29.40 0.245	0.55	1.9
1968a	47	27 - 30	29.00 0.114	0.78	2.7
1968b	10	29 - 31	29.90 0.233	0.74	2.5
1968c	67	27 - 31	29.25 0.101	0.82	2.8
1968d	39	29 - 31	29.51 0.089	0.56	1.9
1972	20	27 - 30	28.80 0.156	0.70	2.4
1973	20	27 - 29	28.30 0.128	0.67	2.0
1993	20	27 - 30	28.35 0.166	0.75	2.6
Pores					
1965	5	44 - 47	44.60 0.600	1.34	3.0
1967a	70	43 - 48	45.67 0.156	1.30	2.9
1967b	5	46 - 47	46.80 0.200	0.45	1.0
1968a	47	42 - 48	45.47 0.201	1.38	3.0
1968b	10	42 - 48	45.20 0.554	1.75	3.9
1968c	65	43 - 48	45.34 0.163	1.31	2.9
1968d	37	42 - 49	45.89 0.247	1.51	3.3
1972	20	43 - 49	45.60 0.400	1.79	3.9
1973	20	43 - 49	45.75 0.315	1.41	3.1
1993	19	44 - 48	45.26 0.227	0.99	2.2
Lamellae					
1965	5	21 - 23	22.00 0.316	0.71	3.2
1967a	70	21 - 25	22.34 0.083	0.70	3.1
1967b	5	22	22.00		
1968a	47	22 - 25	22.19 0.078	0.54	2.4
1968b	10	22 - 23	22.10 0.100	0.32	1.4
1968c	66	20 - 24	22.20 0.070	0.57	2.6
1968d	39	22 - 24	22.28 0.090	0.56	2.5
1972	20	22 - 23	22.29 0.105	0.47	2.1
1973	20	22 - 23	22.10 0.069	0.31	1.4
1993	19	22 - 23	22.16 0.086	0.37	1.7
Granules					
1965	5	94 - 106	101.20 2.059	4.60	4.6
1967a	70	95 - 105	99.36 0.290	2.43	2.4
1967b	5	97 - 100	98.20 0.583	1.30	1.3
1968a	47	93 - 102	98.96 0.284	1.94	2.0
1968b	10	96 - 100	98.00 0.577	1.83	1.9
1968c	66	96 - 106	99.94 0.280	2.27	2.3
1968d	38	96 - 102	99.37 0.265	1.63	1.6
1972	20	97 - 104	100.50 0.495	2.21	2.2
1973	20	94 - 108	100.45 0.745	3.33	3.3
1993	20	97 - 105	100.60 0.499	2.23	2.2

Table 3: *Cnemidophorus*, Oriximiná, analyses of variance, scale counts.

Source	Sum of squares	df	mean square	F
Ventrals				
Between samples	43.4964	9	4.8329	9.406***
Error	150.5505	288	0.5138	
Total	194.0469	302		
Pores				
Between samples	24.5625	9	2.7292	1.431ns
Error	549.0918	288	1.9066	
Total	573.6543	297		
Lamellae				
Between samples	2.3125	9	0.2569	0.818ns
Error	91.4084	291	0.3141	
Total	93.7209	300		
Granules				
Between samples	131.9097	9	14.6566	2.779**
Error	1534.9142	291	5.2746	
Total	1666.8239	300		

Table 4: *Cnemidophorus*, Oriximiná, scale counts, Tukey's test.

Ventrals			Granules		
Sample	m	N	Sample	m	N
1. 1973	28.30	20	1. 1968b	98.00	10
2. 1993	28.35	20	2. 1967b	98.20	5
3. 1965	28.40	5	3. 1968b	98.96	47
4. 1972	28.80	20	4. 1967a	99.36	70
5. 1968a	29.00	47	5. 1968d	99.37	38
6. 1967a	29.04	70	6. 1968c	99.94	66
7. 1968c	29.25	67	7. 1973	100.45	20
8. 1967b	29.40	5	8. 1972	100.50	20
9. 1968d	29.51	39	9. 1993	100.60	20
10. 1968b	29.90	10	10. 1965	101.20	5

Table 5: *Cnemidophorus*, Oriximiná, Tukey's test in temporal sequence.

Sample	Ventrals (m)	Granules (m)	Tail x body (a)	Head x trunk (b)
1965	28.40	101.20	13.27	0.2380
1967a	29.04	99.36	13.76	0.2896
1967b	29.40	98.20	7.34	ns
1968a	29.00	98.96	12.46	0.0912
1968b	29.90	98.00	10.16	0.1913
1968c	29.25	99.94	13.09	0.2268
1968d	29.51	99.37	15.85	0.2303
1972	28.80	100.50	14.22	0.2234
1973	28.30	100.45	12.86	0.2228
1993	28.35	100.60	14.95	0.1829

Table 6: *Cnemidophorus*, Oriximiná, statistics of the regressions of body proportions.

Sample	N	R(x)	R(y)	b	a	F	r ²
Tail x body							
1965	5	35 - 64	83 - 143	1.986 ± 0.2625	15.57 ± 11.087ns	57.230**	0.9502
1967a	32	35 - 71	82 - 160	2.131 0.0586	8.54 4.154*	1324.793***	0.9779
1968a	27	33 - 71	76 - 156	2.005 0.1097	13.84 3.352***	334.162	0.9304
1968b	4	33 - 66	81 - 145	2.117 0.1087	5.07 15.163ns	379.043***	0.9948
1968c	33	32 - 67	77 - 149	2.014 0.0586	13.73 3.700***	1180.752***	0.9744
1968d	16	33 - 55	76 - 129	2.349 0.0685	1.21 4.009ns	1174.279***	0.9882
1972	20	35 - 73	80 - 164	1.957 0.0981	18.01 5.053**	397.719***	0.9567
1973	20	29 - 72	72 - 158	1.983 0.0603	15.18 6.441*	1081.015***	0.9836
1993	20	33 - 70	79 - 157	1.999 0.0657	16.50 5.153	924.892***	0.9809
Tibia x body							
1965	5	35 - 64	6 - 12	0.188 0.0462	-0.35 1.148ns	16.568***	0.8467
1967a	69	35 - 74	6 - 13	0.160 0.0059	9.97 0.230***	742.734***	0.9173
1967b	5	34 - 38	6 - 7	0.087 0.2023	0.185ns	0.185ns	0.8615
1968a	47	33 - 72	6 - 13	0.162 0.0097	10.43 0.235***	279.936***	0.9069
1968b	10	36 - 77	6 - 12	0.154 0.0175	1.01 0.597ns	77.914***	0.9573
1968c	65	32 - 73	5 - 12	0.163 0.0043	8.55 0.235***	1412.892***	0.9363
1968d	39	32 - 67	6 - 12	0.181 0.0078	8.00 0.244**	543.623***	0.9311
1972	20	35 - 73	6 - 12	0.159 0.0102	9.35 0.419***	243.077***	0.9489
1973	20	29 - 72	5 - 12	0.159 0.0087	0.81 0.529ns	333.981***	0.9489
1993	20	33 - 69	6 - 12	0.156 0.0056	1.13 0.403*	783.374***	0.9775
Head x trunk							
1965	5	26 - 49	9 - 15	0.238 0.0270	3.00 1.063ns	77.404***	0.9627
1967a	69	26 - 57	9 - 17	0.220 0.0091	12.93 0.262***	582.373***	0.8968
1967b	5	25 - 29	9	0	indet. (ns)	indet. (ns)	0.4276
1968a	47	24 - 62	9 - 14	0.091 0.0157	11.11 0.200***	33.619***	0.8871
1968b	10	27 - 62	9 - 15	0.191 0.0241	4.54 0.634***	62.839***	0.9494
1968c	67	23 - 54	8 - 17	0.227 0.0065	11.70 0.260***	1219.290***	0.8948
1968d	38	23 - 51	9 - 16	0.230 0.0132	10.97 0.263***	306.326***	0.9301
1972	20	26 - 57	9 - 16	0.223 0.0144	3.45 0.482***	239.617***	0.9699
1973	20	20 - 56	8 - 16	0.223 0.0092	3.51 0.597***	580.107***	0.7567
1993	20	24 - 54	9 - 16	0.183 0.0244	4.90 0.477***	55.992***	0.7567

Table 7: *Cnemidophorus*, Oriximiná, simultaneous comparison of regressions, analyses of variance.

Regression	Source	Sum of squares	df	Mean square	F
Tail x body	general regression	97966.9710	1		
	error	2301.1950	160	14.3825	
	slope	137.9541	9	15.3282	1.066ns
	intercept	336.0906	9	37.3434	2.596***
Tibia x body	general regression	1084.8333	1		
	error	67.4390	277	0.2435	
	slope	1.4893	8	0.1862	0.765ns
	intercept	2.1510	8	0.2689	1.104ns
Head x trunk	general regression	793.9083	1		
	error	123.5007	278	0.4442	
	slope	47.4399	8	5.9300	13.348***

Table 8: *Cnemidophorus*, Oriximiná, statistics of the regressions, Tukey's test.

Intercept, tail x body			Slope, head x trunk		
Sample	a	N	Sample	b	N
1. 1967b	7.34	3	1. 1968a	0.0912	47
2. 1968b	10.16	4	2. 1993	0.1829	20
3. 1968a	12.46	27	3. 1968b	0.1913	10
4. 1973	12.86	20	4. 1967a	0.2196	69
5. 1968c	13.09	33	5. 1973	0.2228	20
6. 1965	13.27	5	6. 1972	0.2234	20
7. 1967a	13.76	32	7. 1968c	0.2268	67
8. 1972	14.22	20	8. 1968d	0.2303	38
9. 1993	14.95	20	9. 1965	0.2380	5
10. 1968d	15.85	16			

Table 9: *Cnemidophorus*, Breves and Corcovado, statistics of the distribution of frequencies of the scale counts.

Sample		N	R	m		s	V	t(B)	t(C x B)
Ventrals									
Breves	1968	50	27 - 29	28.08 ± 0.090		0.63	2.3	2.109*	
	1969	50	27 - 30	28.36	0.100	0.69	2.4		
Corcovado	1965	76	27 - 29	28.30	0.056	0.49	1.7		
	1968	49	27 - 30	28.12	0.080	0.56	2.0		0.312ns
	1969	50	27 - 29	28.32	0.070	0.51	1.8		0.328ns
Pores									
Breves	1968	45	41 - 48	43.73	0.230	1.54	3.5	0.644ns	
	1969	46	40 - 47	43.52	0.234	1.59	3.7		
Corcovado	1965	72	40 - 45	42.65	0.147	1.25	2.9		
	1968	49	40 - 47	43.10	0.183	1.28	3.0		2.166*
	1969	50	41 - 46	42.86	0.159	1.13	2.6		3.173**
Lamellae									
Breves	1968	48	21 - 24	22.21	0.079	0.54	2.5	0.157ns	
	1969	49	22 - 24	22.22	0.067	0.47	2.1		
Corcovado	1965	79	21 - 23	22.04	0.028	0.25	1.1		
	1968	49	21 - 22	21.98	0.020	0.14	0.7		2.845**
	1969	50	21 - 23	21.96	0.049	0.35	1.6		3.195**
Granules									
Breves	1968	50	96 - 106	101.14	0.305	2.16	2.1	2.616**	
	1969	50	94 - 103	100.02	0.300	2.12	2.1		
Corcovado	1965	75	94 - 106	100.29	0.247	2.14	2.1		
	1968	50	94 - 107	102.32	0.286	2.02	2.0		2.981*
	1969	50	95 - 105	100.90	0.309	2.19	2.2		2.133*

Table 10: *Cnemidophorus*, Corcovado, scale counts, analyses of variance.

Source	Sum of squares	df	Mean square	F
Ventrals				
Between samples	1.2344	2	0.6172	2.299ns
Error	46.1836	172	0.2685	
Total	47.4319	174		
Pores				
Between samples	5.9063	2	2.9531	1.978ns
Error	250.8359	168	1.4931	
Total	256.7422	170		
Lamellae				
Between samples	0.2109	2	0.1055	1.565ns
Error	11.7871	175	0.0674	
Total	12.0000	177		
Granules				
Between samples	124.6250	2	62.3125	13.819***
Error	775.0000	172	4.5058	
Total	899.6250	174		

Table 11: *Cnemidophorus*, Corcovado, Tukey's test.

Sample	m	N	Sample	b	N	Sample	b	N
Granules			Tail x body			Tibia x body		
1965	100.29	75	1969	1.913	11	1965	0.160	78
1969	100.90	50	1965	2.146	21	1968	0.169	47
1968	102.32		1968	2.282	22	1969	0.189	50

Table 12: *Cnemidophorus*, Breves and Corcovado, statistics of the regressions of body proportions.

Sample	N	R(x)	R(y)	b	a	F	R ²
Tail x body							
Breves	1968 20	32 - 74	70 - 163	2.121 ± 0.0682	7.81 ± 5.632ns	968.096***	0.9817
	1969 24	32 - 69	75 - 146	2.090 0.0875	9.98 4.507*	570.535***	0.9629
Corcovado	1965 21	32 - 60	72 - 132	2.146 0.0703	5.01 4.510ns	932.923***	0.9800
	1968 22	31 - 66	73 - 152	2.282 0.0563	0.04 4.891ns	1649.538***	0.9880
	1969 11	35 - 65	85 - 143	1.913 0.1054	17.79 5.418**	328.902***	0.9734
Tibia x body							
Breves	1968 50	32 - 74	6 - 12	0.162 0.0042	8.48 0.290***	1485.653***	0.9687
	1969 50	32 - 73	6 - 13	0.183 0.0056	9.58 0.216***	1085.894***	0.9577
Corcovado	1965 78	30 - 75	6 - 12	0.160 0.0063	7.13 0.186***	584.708***	0.8850
	1968 47	31 - 69	5 - 12	0.169 0.0053	8.17 0.293***	1015.490***	0.9576
	1969 50	29 - 72	6 - 16	0.189 0.0068	8.62 0.327***	766.154***	0.9410
Head x trunk							
Breves	1968 48	23 - 57	8 - 17	0.230 0.0070	11.56 0.345***	1088.971***	0.9595
	1969 50	23 - 60	9 - 17	0.239 0.0074	12.66 0.307***	1056.917***	0.9566
Corcovado	1965 78	21 - 58	8 - 17	0.236 0.0089	9.94 0.217***	707.796***	0.9030
	1968 50	23 - 53	8 - 16	0.245 0.0068	11.64 0.340***	1291.109***	0.9642
	1969 49	21 - 56	8 - 16	0.228 0.0069	11.49 0.317***	1101.633***	0.9591

Table 13: *Cnemidophorus*, Breves, differences between regressions, 1968 and 1969.

Regression	Slope difference (b)		df	t	Intercept difference (a)		df	t
Tail x body	0.0308 ± 0.09091		40	0.339ns	12.97 ± 3.911		41	3.316**
Tibia x body	0.0209	0.00699	96	2.991*				
Head x trunk	0.0093	0.01110	94	0.845ns	0.97 0.466		95	2.082*

Table 14: *Cnemidophorus*, Corcovado, simultaneous comparisons of regressions, analyses of variance.

Regression	Source	Sum of squares	df	Mean square	F
Tail x body	general regression	23473.3554	1		
	error	385.7891	48	8.0373	
	slope	82.5349	2	41.2674	5.135**
Tibia x body	general regression	657.8848	1		
	error	45.4580	169	0.2690	
	slope	2.8506	2	1.4253	5.299**
Head x trunk	general regression	850.4820	1		
	error	45.5746	171	0.2665	
	slope	0.6636	2	0.3318	1.245ns
	intercept	0.1612	2	0.0806	0.302ns

Table 15: *Cnemidophorus*, Alter do Chão, statistics of the distributions of frequencies of the scale counts.

Sample	Sex	N	R	m	s	V	t
Ventrals							
1968a	♂	30	27 - 30	28.10 ± 0.130	0.71	2.5	2.114*
	♀	30	27 - 30	28.47 0.115	0.63	2.2	
1968b	♂	30	27 - 30	28.40 0.132	0.72	2.6	0.356ns
	♀	32	27 - 31	28.31 0.203	1.15	4.1	
1969	♂	30	27 - 30	28.27 0.166	0.91	3.2	0.629ns
	♀	30	27 - 30	28.40 0.132	0.72	2.6	
Pores							
1968a	♂	29	42 - 51	47.69 0.450	2.42	5.1	3.280**
	♀	25	41 - 51	45.56 0.466	2.33	5.1	
1968b	♂	27	43 - 51	47.15 0.426	2.21	4.7	5.201***
	♀	27	41 - 48	44.26 0.356	1.85	4.2	
1969	♂	27	44 - 51	47.26 0.409	2.12	4.5	4.746***
	♀	27	41 - 48	44.63 0.374	1.94	4.4	
Lamellae							
1968a	♂	30	19 - 22	21.00 0.166	0.91	4.3	0.144ns
	♀	30	19 - 22	20.97 0.162	0.89	4.2	
	♂♀	60	19 - 22	20.98 0.115	0.89	4.3	
1968b	♂	31	19 - 22	20.71 0.192	1.07	5.2	0.679ns
	♀	32	19 - 22	20.53 0.180	1.02		
	♂♀	63	19 - 22	20.62 0.131	1.04	5.0	
1969	♂	30	19 - 22	20.63 0.182	1.00	4.8	0.267ns
	♀	30	19 - 22	20.57 0.171	0.94	4.6	
	♂♀	60	19 - 22	20.60 0.124	0.96	4.7	
Granules							
1968a	♂	30	97 - 110	103.70 0.685	3.75	3.6	4.921***
	♀	26	93 - 107	98.96 0.667	3.40	3.4	
1968b	♂	30	95 - 111	102.27 0.708	3.88	3.8	6.424***
	♀	32	92 - 103	96.69 0.517	2.92	3.0	
1969	♂	30	91 - 112	101.67 0.785	4.30	4.2	5.393***
	♀	29	90 - 103	96.48 0.543	2.92	3.0	

Table 16: *Cnemidophorus*, Alter do Chão, scale counts, analyses of variance.

Source	Sum of squares	df	Mean square	F
Ventrals ♂♂				
Between samples	1.3594	2	0.6797	1.010ns
Error	53.7656	87	0.6180	
Total	55.1250	89		
Ventrals ♀♀				
Between samples	0.3720	2	0.1860	0.245ns
Error	67.5410	89	0.7589	
Total	67.9130	91		
Pores ♂♂				
Between samples	4.6287	2	2.3144	0.453ns
Error	408.7930	80	5.1099	
Total	413.4217	82		
Pores ♀♀				
Between samples	23.1189	2	11.5595	2.766ns
Error	317.6406	76	4.1795	
Total	340.7595	78		
Lamellae ♂♀				
Between samples	5.6396	2	2.8198	2.016ns
Error	168.2402	180	0.9347	
Total	173.8798	182		
Granules ♂♂				
Between samples	65.4787	2	32.7394	2.063ns
Error	1380.8435	87	15.8718	
Total	1446.3222	89		
Granules ♀♀				
Between samples	103.1361	2	51.5680	5.462**
Error	793.0938	84	9.4416	
Total	896.2299	86		

Table 17: *Cnemidophorus*, Alter do Chão, statistics of the regressions of body proportions.

Sample	Sex	N	R(x)	R(y)	b	a	F	r ²	t(b)	t(a)
Tail x body										
1968a	♂	9	43 - 72	112 - 165	1.804 ± 0.1654	32.46 ± 6.211**	118.967***	0.9444	6.958***	
	♀	5	34 - 61	81 - 130	1.779 0.3308	24.58 9.585ns	28.922*	0.9060	0.566ns	4.664***
1968b	♂	9	35 - 58	82 - 143	2.649 0.1242	-12.49 6.668ns	455.022***	0.9848		
	♀	11	30 - 49	64 - 119	2.707 0.1308	-15.60 5.295*	428.068***	0.9794		
1969	♂	9	41 - 61	99 - 143	2.079 0.2638	17.53 4.760***	62.081***	0.8987	0.653ns	2.953*
	♀	5	38 - 57	88 - 126	2.188 0.3130	4.72 7.501ns	48.885**	0.9422		
Tibia x body										
1968a	♂	30	43 - 77	8 - 15	0.170 0.0138	11.93 0.307***	153.452***	0.8457	1.751ns	1.632ns
	♀	28	34 - 62	7 - 12	0.140 0.0161	10.71 0.214***	75.218***	0.7431	1.495ns	0.525ns
1968b	♂	29	30 - 67	5 - 14	0.221 0.0079	9.28 0.476***	774.364***	0.9663		
	♀	31	30 - 75	5 - 15	0.205 0.0103	8.84 0.363***	398.387***	0.9321	2.601*	
1969	♂	30	31 - 69	6 - 14	0.210 0.0071	10.00 0.395***	863.184***	0.9686		
	♀	30	31 - 60	6 - 11	0.189 0.0058	8.77 0.334***	1055.204***	0.9742		
Head x trunk										
1968a	♂	29	32 - 55	11 - 19	0.398 0.0279	15.83 0.505***	203.094***	0.8827	4.563***	
	♀	28	25 - 43	9 - 15	0.243 0.0238	13.39 0.278***	104.525***	0.8808	1.587ns	0.229ns
1968b	♂	27	22 - 49	8 - 18	0.327 0.0149	12.56 0.565***	477.350***	0.9502		
	♀	31	22 - 55	8 - 20	0.292 0.0177	11.74 0.413***	270.603***	0.9032	3.102*	
1969	♂	27	22 - 51	9 - 18	0.287 0.0129	13.04 0.452***	491.566***	0.9516		
	♀	30	22 - 46	9 - 15	0.241 0.0093	11.73 0.347***	671.5334***	0.9600		

Table 18: *Cnemidophorus*, Alter do Chão, simultaneous of regressions, analyses of variance.

Regression	Source	Sum of squares	df	Mean square	F
Tail x body	♂♂	General regression	10267.8040	1	
		Error	333.6982	21	15.8904
		Slope	201.4699	2	100.6850
	♀♀	General regression	7233.6069	1	
		Error	283.4175	15	18.8945
		Slope	190.5300	2	95.2650
Tibia x body	♂♂	General regression	474.6194	1	
		Error	21.4250	83	0.2581
		Slope	3.4671	2	1.7336
	♀♀	General regression	285.5668	1	
		Error	16.5767	83	0.1997
		Slope	2.8588	2	1.4294
Head x trunk	♂♂	General regression	665.5556	1	
		Error	38.5107	77	0.5001
		Slope	7.6053	2	3.8027
	♀♀	General regression	314.2354	1	
		Error	26.4998	83	0.3193
		Slope	2.3051	2	1.1526

Table 19: *Cnemidophorus*, Alter do Chão, Tukey's test.

♂♂ Sample		♀♀ Sample	
		Granules	
		m	
		1968a	98.96
		1968b	96.69
		1969	96.48
Tail x body		b	
1968a	1.804	1968a	1.779
1969	2.649	1969	2.188
1968b	2.649	1968b	2.707
Tibia x body			
1968a	0.170	1968a	0.140
1969	0.210	1969	0.189
1968b	0.221	1968b	0.205
Head x body			
1969	0.287	1969	0.241
1968b	0.327	1968a	0.243
1968a	0.398	1968b	0.292

Table 20: *Cnemidophorus*, temporal changes.

Character	Locality	Breves	Corcovado	Alter do Chão
	Oriximiná			
Ventrals	1968b 1972	1968/1969	-	-
Granules	0	1968/1969	1968	♀♀ 1968a/b
Tail x body	(b) - (a) 1967a/b	- 1968/1969	1968/1969 0	♂♀ 1968/1969 0
Tibia x body	(b) - (a) -	1968/1969 0	1968/1969 0	♂♀ 1968a/b 0
Head x trunk	(b) 1967a/b (a) 0	- 1968/1969	- -	♂♂ 1968a/b ♀♀ 1968/1969 0

Note: 0 = does not apply; - = no change.